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coral reef paper

Pacific-wide pH snapshots reveal that high coral cover correlates with low, but variable pH

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ABSTRACT.—Ocean acidification (OA) is impairing the construction of coral reefs while simultaneously accelerating their breakdown. The metabolism of different reef organism assemblages alters seawater pH in different ways, possibly buffering or exacerbating OA impacts. In spite of this, field data relating benthic community structure and seawater pH are sparse. We collected pH time-series data snapshots at 10 m depth from 28 different reefs (n = 13 lagoon, n = 15 fore reef) across 22 Pacific islands, spanning 31° latitude and 90° longitude. Coincident with all deployments, we measured percent cover of the benthic community. On fore reefs, high coral cover (CC) negatively correlated with mean and minimum pH, but positively correlated with pH variability. Conversely, pH minima were positively correlated to coverage of coralline and turf algae. Benthic cover did not correlate with pH in lagoonal reefs. From 0% to 100% CC, mean pH and aragonite saturation state (Ω_{arag}) declined −0.081 and −0.51, respectively, while declines in minimum values were greater (Δmin pH = −0.164, Δmin Ω_{arag} = −0.96). Based upon previously published relationships, the mean pH decline from 0% to 100% CC would depress coral calcification 7.7%–18.0% and increase biologically-mediated dissolution 13.5%–27.9%, with pH minima depressing dark coral calcification 14.4%–35.2% and increasing biologically-mediated dissolution 31.0%–62.2%. This spatially expansive dataset provides evidence that coral reefs with the highest coral cover may experience the lowest and most extreme pH values with OA.

Climate change and ocean acidification (OA) are negatively impacting coral reefs (Albright et al. 2018, Hughes et al. 2018). While the alarm over warming on coral reefs was sounded nearly 30 years ago (Glynn 1991), the concern over OA has received

considerable attention only in the past 10–15 years. OA depresses coral and net reef calcification, stimulates biologically-mediated chemical dissolution, and negatively impacts noncalcareous organisms such as fishes (Munday et al. 2010, Chan and Connolly 2013, Enochs et al. 2015a, 2016a,b, Albright et al. 2018). The accretion rates of coral reef framework structures, which are a vital habitat supporting high biodiversity of organisms, are just slightly greater than rates of erosion on healthy reefs (Glynn and Manzello 2015). As such, any disturbance stimulating bioerosion or lessening calcification has negative ramifications for the persistence of reef frameworks.

Because OA is a relatively new discipline, the rush for information has resulted in systemic and repeated research errors. Most experiments have been pseudoreplicated (Cornwall and Hurd 2016), early studies altered seawater CO_2 inappropriately by using acid addition rather than CO_2 bubbling (e.g., Langdon and Atkinson 2005), and the role of natural variability remains poorly understood (Rivest et al. 2017). The relevance of single-species experiments to real-world ecological function and interactions (predation, herbivory, competition, etc.) is unclear, and the short time scales of lab experiments relative to the slow progression of OA also limits extrapolation of results. With new legislation and global mandates, global OA observing networks are beginning to provide necessary and valuable information on the rate and magnitude of OA progression at select sites (Newton et al. 2015). However, there is presently only one instrument that consistently provides accurate and precise measurement of a seawater CO_2 variable for >2–3 mo without active human intervention, but this is limited to surface waters, includes only one CO_2 parameter [partial pressure of CO_2 (pCO_2)], and is prohibitively costly (Sutton et al. 2014). The Durafet pH sensor has shown promise, with reports of sensor stability, as well as accurate and precise measurements of pH for up to 9 mo in the field (Bresnahan et al. 2014, Gonski et al. 2018). However, this sensor's performance is highly limited by biofouling and requires land-based calibration procedures, as well as independent means of quality control throughout deployment (i.e., regular collection of bottle samples that can be analyzed for pH in the lab; Bresnahan et al. 2014). In our experience, sensors typically provide quality data for up to 3 mo before biofouling and fine sediment accumulation on the sensor cause the instrument to fail (Manzello, unpub data). Thus, in situ, benthic CO_2 data from coral reef environments are highly limited and much of the knowledge of CO_2 variability of reefs comes from labor and time-intensive hand collection of seawater samples and laboratory titrations (e.g., Shaw et al. 2012). This important knowledge gap needs to be addressed, as the diurnal range of seawater CO_2 is increasing as OA progresses because the buffering capacity of seawater is declining as the oceans absorb more CO_2 (Shaw et al. 2013a).

It has been long understood that the benthic community composition of shallow marine ecosystems alters the chemistry of the overlying water column, leading to the frequently used techniques that approximate reef "metabolism" by measuring changes in seawater chemistry over time and/or space (Odum and Odum 1955). The carbon cycle on coral reefs is driven by organic carbon metabolism (photosynthesis and respiration) and inorganic carbon metabolism [precipitation and dissolution of calcium carbonate ($CaCO_3$)]. Total CO_2 (TCO_2) is decreased by 1 mole due to the production of 1 mole of organic matter or $CaCO_3$. On the other hand, TCO_2 increases by 1 mole due to the dissolution of 1 mole of $CaCO_3$ or oxidation of organic carbon via respiration. The organic carbon metabolism that normally occurs on a reef does not significantly change the total alkalinity (TA) of seawater (Gattuso et al. 1999). TA is

affected by inorganic carbon metabolism and is decreased by 2 equivalents for every mole of $CaCO_3$ produced and increased by 2 equivalents for every mole dissolved. In the simplest sense, photosynthesis and dissolution raise pH whereas respiration and calcification depress pH. During the day, photosynthesis and calcification are the dominant processes on coral reefs whereas at night, respiration and dissolution become more important (Kinsey 1985).

Recent headway has been made to understand benthic community feedbacks on seawater CO_2 (Anthony et al. 2011, 2013). In mesocosms, corals have been shown to lower seawater pH and aragonite saturation state (Ω_{arag}) due to the elevation of CO_2 associated with calcification (Anthony et al. 2013). Conversely, macroalgae and seagrasses take up CO_2, elevating pH and Ω_{arag} (Manzello et al. 2012, Anthony et al. 2013). This has led to the hypothesis that coral-dominated areas may exacerbate OA, whereas algae or seagrasses may buffer OA impacts in downstream habitats, but clear patterns have not always emerged. Daytime increases in Ω_{arag} and pH in fleshy algae and mixed communities were observed in Hawaii (Page et al. 2016), but in a companion study differences in CO_2 variability or community metabolism were not detected in coral reef mesocosm studies (40%–80% live coral) from Bermuda (Page et al. 2017).

Coral reefs that are net calcifying have been well documented to experience depressed pH diurnally and seasonally (Shaw et al. 2012, Albright et al. 2015, Yeakel et al. 2015). Field studies explicitly linking the magnitude of this natural acidification to benthic cover of key taxa are limited. Most research relating different coverage of key benthic taxa to pH variability has occurred in mesocosm or modeling studies. There was an increased diel range in pCO_2 with increasing coral cover at buoy sites in Bermuda (n = 2) and Hawaii (n = 1; Page et al. 2016), but these sites spanned depths from 2 to 11 m and encompassed different reef zones (lagoon, rim reef, back reef). Price et al. (2012) deployed SeaFET pH sensors at 6 sites (n = 4 fore reef, n = 2 reef terrace) across 3 islands spanning 7° of latitude. They found a significant correlation between pH values above seasonal climatological lows and the percent cover and accretion rate of noncoral calcifiers on recruitment tiles, with fleshy, noncalcified organisms dominating at low pH.

In this study, we deployed high-accuracy, low-drift pH sensors at 28 different coral reef sites (n = 13 lagoon, n = 15 fore reef) across 22 islands and 9 archipelagos in the Pacific Ocean, spanning 31° of latitude and 90° of longitude (Fig. 1, Online Table S1). These deployments were done as part of the Global Reef Expedition (GRE) undertaken by the Khaled bin Sultan's Living Ocean's Foundation from 2011 to 2015 (Global Reef Expedition 2018). The GRE mapped and characterized remote coral reef sites with minimal anthropogenic impact. The overarching goal was to identify status and threats, as well as examine factors that promote resilience from major disturbance events to aid in local management and conservation. As one component of this effort, we sought to better understand the relationship between seawater pH variability and benthic community structure.

Materials and Methods

Instrument Deployment and Calibration.—SeaFET pH sensors were temporarily secured to the reef substrate using rebar and cable ties (Fig. 1). We picked a representative area of reef framework within the survey site, using care to minimize

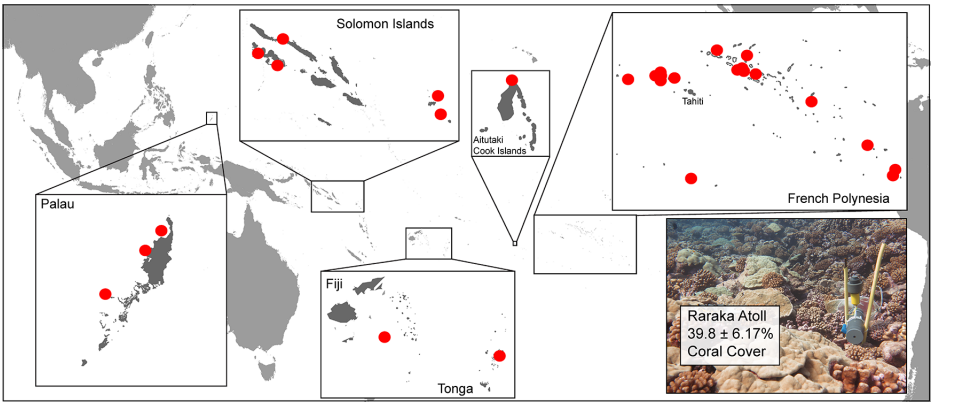

Figure 1. Map showing location of SeaFET pH deployments in French Polynesia, Fiji, Tonga, Solomon Islands, and Palau. Image overlain shows SeaFET pH deployed at Raraka Atoll, French Polynesia.

any damage to living coral. The SeaFET was placed on the substrate such that the sensor was within 10 cm of the benthos (Fig. 1). Instruments were deployed at a targeted depth of 10 m [mean (SE) = 10.8 m (0.30)] from 1.02 to 9.21 d [2.65 d (0.376)] on 28 reefs (Online Table S1). Temperature and pH data were collected at 15–30 min intervals. For each deployment, we calculated mean, standard deviation, minimum, maximum, and range of pH and temperature. As discussed in Gonski et al. (2018), this sensor has proven to be highly accurate and precise in the marine environment due to its quick response time, linear response with temperature, and excellent signal stability. It has been proven effective in coastal waters, the open ocean, laboratory settings, near-zero temperatures, low ionic strength seawater, and estuarine environments. We took great care to follow established best practices for instrument deployment, calibration, and validation. All instruments were factory calibrated prior to cruise deployments and calibration/validation bottle samples were taken in concert with all deployments to verify sensor accuracy and stability. In this instance, the short-term nature of our deployments (1–9 d) is a strength with regard to the uncertainty of our data, given that our experience has shown that biofouling and accumulation of fine sediments generally are what drive sensor values to deviate from reality.

SeaFET data were calibrated with bottle samples that were taken at the beginning and end of sensor deployments. Seawater was collected on SCUBA in borosilicate (500 ml) bottles adjacent to the SeaFET and then fixed with 200 µl $HgCl_2$ upon reaching the surface. Bottle pH was calculated from measurement of TA and TCO_2 as described in Enochs et al. (2015b). Samples were transported to NOAA's Atlantic Oceanographic and Meteorological Laboratories (AOML), where they were analyzed for dissolved inorganic carbon (DIC) and TA using autotitrators (AS-C3 and AS-ALK2 respectively, Apollo SciTech). The accuracy and precision of the TCO_2 and TA measurements were always <4 and 2 µmol kg^{-1} and 3 and 2 µequiv kg^{-1}, respectively, and were verified with certified reference materials distributed by A Dickson (Scripps Institute of Oceanography). The pH offset (bottle pH – SeaFET pH) was determined for every bottle. For each cruise, these offsets were plotted in chronological order to determine if there was sensor drift over time (i.e., the presence of a downward or upward trend in the offsets). The mean offset of all bottle samples was used as

the correction value for all SeaFET data for that cruise, unless there was noticeable drift, whereby an individual offset was applied for every SeaFET deployment based on the mean offset of the bottle samples at the beginning and end of that particular deployment. The bottle samples and SeaFET values were within ± 0.05 pH units for 89.3% of the deployments, and the maximum deviation between the bottle sample and SeaFET was a −0.0911 offset (TOHA04, Online Table S2).

Benthic Surveys.—At each site, the percent cover of benthic organisms and substrate types was assessed along 10 m transects using a point intercept method where the organism and substrate were recorded every 10 cm for 100 points per transect. On average, four transects were assessed per site [mean (SE) = 4.1 (0.31), Online Table S3]. The major functional groups identified were subdivided into stony corals (identified to genus), other sessile invertebrates (identified to phylum or class), and algae (subdivided into macroalgae, coralline algae, turf algae). For this analysis, data were pooled into total live cover of coral (pooled species), macroalgae, turf algae, and coralline algae.

Data and Statistical Analysis.—Data were split into lagoon (n = 13 sites) and fore reef (n = 15) to account for the effect of different hydrodynamic regimes on coral reef carbonate chemistry dynamics (e.g., Falter et al. 2013). We compared pH, temperature, and benthic cover of the lagoon and fore reefs using t-tests when data were normal and homoscedastic or Mann–Whitney U tests when these assumptions were not met. Given that pH is a function of temperature, we also calculated pH at 25 °C using the simple relationship of Lui and Chen (2017). Pearson correlation (Spearman if assumptions not met) was used to determine if pH and temperature were correlated with benthic cover. When a significant correlation was identified, the relationship was examined graphically to determine if there were outliers in the dataset. When there were outliers, these were removed and the correlation test was rerun to determine if the outliers were influencing the trends. If the removal of one outlier led to the correlation becoming insignificant, then we assumed the correlation was spurious. If there were no clear outliers, or if the removal of an outlier did not impact the significance of the correlation, linear regression analysis was conducted. All statistical analysis was conducted in SigmaPlot 12.

Modeling Future Conditions and Organismal Response.—In order to compare coral cover to pH measurements, we calculated Ω_{arag} and pCO_2 for the corresponding pH measurements. The linear regressions of coral cover (CC, %) with mean and minimum pH are as follows: Mean pH = 8.066 – 0.000838 × CC; Min pH = 8.046 – 0.00164 × CC. At 0% CC, mean and minimum pH = 8.066 and 8.046, respectively, whereas at 100% CC, these are 7.982 and 7.882, respectively. Based on the measured regressions of coral cover with mean and minimum pH, we then input the minimum and mean pH at 0%, 25%, 50%, 75%, and 100% CC into CO2SYS using the following means of all bottle samples that were paired with SeaFET deployments (n = 38): temperature = 27.7 °C, salinity = 34.8, TA = 2317.5 μequiv kg^{-1}, TCO_2 = 1982.2 μmol kg^{-1}, pH (total scale) = 8.062, pCO_2 = 379.2 μatm, and Ω_{arag} = 3.83. This provided estimated mean and minimum values of TCO_2, pCO_2, and Ω_{arag} at these levels of CC under present day conditions.

To model mean and minimum pH, pCO_2, and Ω_{arag} with OA as a function of CC, we calculated future conditions from 0% to 100% coral cover by adding (1) the OA-induced change in pCO_2 to the (2) CC-induced change in pCO_2 for each time point and coral cover value, while holding TA constant and using the same mean bottle values for temperature and salinity. We assumed that each 1 ppm increase in atmospheric pCO_2 corresponded to a 1 µatm increase in seawater pCO_2. For example, the mean ΔpCO_2 from 0% to 100% coral cover is +98.1 µatm based on the measured mean ΔpH of −0.081. To estimate what the mean pCO_2 of a coral reef with 100% CC under a 2× CO_2 scenario (atmospheric pCO_2 = 560 ppm, +155 ppm assuming present day pCO_2 = 405 ppm), we added 155 µatm pCO_2 to represent OA plus an additional 98.1 µatm pCO_2 to represent 100% CC. For 0% CC, we simply added the 155 µatm pCO_2. The model was also run at pH_{25}.

Given that the ΔpCO_2 due to varying levels of coral cover is due to coral metabolism and rates of coral metabolism will change with OA, the magnitude of the resultant ΔpCO_2 will likely change with OA, but for simplicity we assumed it was constant in our OA projections. The diurnal and seasonal variation in pH caused by photosynthesis and respiration will be amplified as the oceans lose buffering capacity as they uptake more CO_2 due to the Revelle factor, thus pH variability driven by reef metabolism will increase (e.g., Shaw et al. 2013b). Our model is highly conservative because it does not reflect the Revelle factor given that we modified pCO_2 as opposed to TCO_2 in our projections. This simplistic approach was adopted due to all the unknowns associated with estimating rates of reef metabolism in the future. For instance, it is unclear if corals and other reef-associated organisms will be able to adapt and/or acclimate to OA (e.g., Camp et al. 2016, Cornwall et al. 2020). Furthermore, feedback mechanisms that exist in nature, such as diurnal variability offsetting OA sensitivities (Enochs et al. 2018), have not been appropriately considered in laboratory experiments. The model also assumes that the ΔpH with coral cover is due to increasing TCO_2 as we held TA constant to estimate the corresponding changes in the other carbonate parameters. This too was done for simplicity as the ΔpH is presumably driven by changes in both TA and TCO_2 due to reef metabolism (photosynthesis, respiration, calcification, dissolution). We explored how much bias the assumption of constant TA could introduce by holding TCO_2 constant rather than TA when inputting the various values of pH as described above. The difference in calculated mean Ω_{arag} and pCO_2 were 0.07 and 9.3 µatm, respectively, when TCO_2 was held constant rather than TA, thus the bias by holding TA constant is negligible.

To estimate how much the decline in pH with increasing CC would correspond to percent declines in coral calcification, we used the first order calcification model (Langdon and Atkinson 2005) and the results of the meta-analysis of Chan and Connolly (2013). The Chan and Connolly (2013) estimate is conservative and suggests that there will only be a 15% decline in coral calcification per unit decline in Ω_{arag}. We also explored how the pH changes due to CC would impact other CO_2 sensitive taxa such as coralline algae and bioeroders using the same models of Enochs et al. (2015a). The clionaid sponge function used was for the Caribbean species, *Pione lampa*; this was used because the magnitude of the response to OA was essentially identical to the Pacific species *Cliona orientalis* (Wisshak et al. 2012). *Pione lampa* is also azooxanthellate, thus removing any interaction response due to algal symbionts (Fang et al. 2014). The bioeroder response curves are based on single-experiments as

described in Enochs et al. (2015a), as opposed to the pooled results of multiple species for coral calcification.

It has been argued that values of pH cannot be averaged directly but should be back-calculated to values of hydrogen ion concentration [H^+], averaged, and then retransformed to pH values (Barth 1975). This is because pH is a measure of the negative log transformation of [H^+]. However, later work showed that this was most important over large ranges in pH (pH range >1) or when mixing solutions with large differences in pH that do not contain natural buffers (Boyd et al. 2011). Over small pH ranges, the difference between averaging pH vs averaging [H^+] is mathematically less important. Most scientists use average pH, thus for comparisons with previous studies, it is generally most appropriate to use direct pH averages. This is especially true when regression equations that estimate a biological response to pH are based on direct pH measurements (Boyd et al. 2011), which is the case with the data reported herein.

To verify that our calculation of mean pH was acceptable, we followed the suggestion of Barth (1975) and compared our mean pH values with mean pH values that had been retransformed from mean [H^+] values (Online Table S4). Mean pH values calculated these two ways showed little difference; the average difference (SD) was 0.0006 (0.00067), which is outside the uncertainty and precision of the raw data measured. Furthermore, the regression statistics using the two metrics for mean pH as a function of coral cover were nearly identical (Online Table S5). Barth (1975) further suggested that using median pH and the range in pH were preferable to mean pH and the standard deviation of pH. Using these variables showed the same trends and patterns as using mean pH and the standard deviation of the measured pH values (Online Table S5), thus we utilized mean and standard deviation of the pH values as measured rather than using values back calculated from [H^+]. Interestingly, the intercept of the median pH linear regression was identical to that derived from the regression of mean pH with coral cover.

Results

The mean (SE) pH pooled for all lagoon sites [8.029 (0.112)] was lower than the fore reefs [8.039 (0.006)], but this was not significant (Table 1). The only significant difference between the two habitats was that maximum pH values were higher at the fore reef sites [8.096 (0.011)] than the lagoonal sites [8.062 (0.012); Table 1]. Mean (SE) pH by site ranged from 7.932 (0.0237) at Hao Atoll lagoon in French Polynesia to 8.120 (0.0239) at Ha'apai lagoon in Tonga (Online Table S2). The lagoons were warmer with mean, minimum, and maximum temperatures that were higher by 1 °C (Table 1, Online Table S2). When pH was normalized to 25 °C, values between the lagoon and fore reef were very similar and there were no differences between them. Mean (SE) percent cover of coralline algae was significantly higher on the fore reefs [30.1% (3.69)] vs the lagoon sites [19.3% (4.04)], but there were no other differences in benthic cover between the lagoon and fore reefs (Table 1). The percent cover of scleractinian corals ranged from 2.7% to 67.3% at the lagoon sites [mean (SE) = 32.0% (6.14)] and 6.3% to 63.8% on the fore reefs [31.7% (5.09); Online Table S3].

On the fore reefs, coral cover (CC) was positively related to the standard deviation (SD) in pH ($R^2 = 0.57$, $P < 0.01$) and pH range ($R^2 = 0.54$, $P < 0.01$), but negatively

Table 1. Comparison of pH_{insitu}, pH_{25}, temperature, and benthic cover between lagoon and fore reef environments. A *t*-test was used when data were normal and homoscedastic, whereas a Mann–Whitney *U* test was used when these assumptions were not met.

Variable	Lagoon	Fore reef	Significance
pH_{insitu}			
Mean	8.029 (0.0112)	8.039 (0.006)	ns
SD	0.017 (0.0020)	0.022 (0.0033)	ns
Min	7.984 (0.0131)	7.994 (0.0093)	ns
Max	8.062 (0.0120)	8.096 (0.011)	$U = 39.5$, $P < 0.01$: Fore reef > Lagoon
Range	0.077 (0.0109)	0.102 (0.0168)	ns
pH_{25}			
Mean	8.081 (0.0087)	8.077 (0.0077)	ns
SD	0.018 (0.0022)	0.023 (0.0033)	ns
Min	8.035 (0.0124)	8.031 (0.0098)	ns
Max	8.115 (0.0089)	8.133 (0.0121)	ns
Range	0.080 (0.0119)	0.103 (0.0169)	ns
Temperature			
Mean	28.47 (0.384)	27.5 (0.28)	$t = 2.09$, $P < 0.05$: Lagoon > Fore reef
SD	0.127 (0.0242)	0.145 (0.025)	ns
Min	28.21 (0.420)	27.1 (0.32)	$t = 2.15$, $P < 0.05$: Lagoon > Fore reef
Max	28.76 (0.334)	27.8 (0.28)	$t = 2.21$, $P < 0.05$: Lagoon > Fore reef
Range	0.56 (0.114)	0.71 (0.147)	ns
Benthic cover			
Coral	32.0 (6.14)	31.7 (5.09)	ns
Macroalgae	6.5 (1.59)	7.7 (1.46)	ns
Turf algae	30.3 (3.37)	26.4 (4.43)	ns
Coralline algae	19.3 (4.04)	30.1 (3.69)	$t = 1.96$, $P < 0.05$: Fore reef > Lagoon

Table 2. Linear regression statistics. SD = standard deviation; CC = coral cover; CAC = coralline algae cover; Turf = turf algae cover.

Equation	R^2	*F*	*P*-value
pH_{insitu}			
Mean = 8.066 − 0.000838 × CC	0.51	13.5	<0.01
SD = 0.00669 + 0.000489 × CC	0.57	17.5	<0.01
Min = 8.046 − 0.00164 × CC	0.81	54.3	<0.001
Range = 0.0248 + 0.00242 × CC	0.54	15.2	<0.01
Min = 7.95 + 0.00146 × CAC	0.34	6.6	<0.05
Min = 7.965 + 0.00108 × Turf	0.27	4.7	<0.05
pH_{25}			
SD = 0.00762 + 0.000469 × CC	0.53	14.6	<0.01
Min = 8.076 − 0.00143 × CC	0.55	16.2	<0.01
Range = 0.0275 + 0.00236 × CC	0.51	13.5	<0.01
Mean = 8.04 − 0.00123 × CAC	0.34	6.8	<0.05
Min = 7.977 + 0.00178 × CAC	0.45	10.8	<0.01

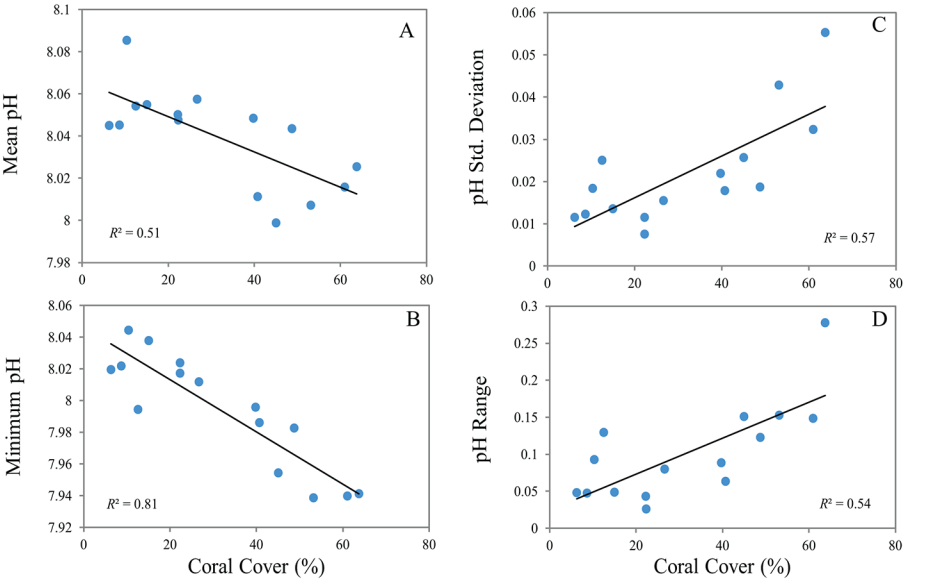

Figure 2. Seawater pH as a function of coral cover (%) for fore reefs. (A) Mean, (B) minimum, (C) standard deviation, and (D) range of pH plotted against coral cover. Black line illustrates significant linear regression.

related to mean (R^2 = 0.51, P < 0.01) and minimum pH (R^2 = 0.81, P < 0.001; Table 2, Fig. 2). In an opposite pattern to CC, coralline and turf algae cover was positively related to minimum pH (Fig. 3). There were no relationships between benthic cover and pH variability at the lagoon sites because the correlations with macroalgae cover were driven by a single outlier in the dataset (Online Fig. S1). The overall low macroalgae cover of all sites may explain the lack of any relationships between macroalgae cover and pH variability. When pH was normalized to 25 °C, the same correlations between coral cover and minimum, standard deviation, and range in pH existed (Online Fig. S2), but the correlation with mean pH was no longer significant (Online Table S6). The correlation between pH and turf algae also became nonsignificant.

Based upon the linear regressions, differences in mean pH, Ω_{arag}, and pCO_2 from 0% to 100% CC were −0.081, −0.51, and −98.1 µatm, respectively (Fig. 4). The changes in minimum values from 0% to 100% CC were greater, as Δmin pH = −0.164, Δmin pCO_2 = −231.0, and Δmin Ω_{arag} = −0.96 (Fig. 4). The changes in minimum values from 0% to 100% CC when temperature was normalized to 25 °C were similar and Δmin pH = −0.143, Δmin pCO_2 = −180.3, and Δmin Ω_{arag} = −0.82. The decrease in magnitude of the pH and Ω_{arag} decline with increasing OA is due to the nonlinear response between pCO_2 and these two variables. At 2× CO_2 (atmospheric pCO_2 = 560 ppm) and 3× CO_2 (840 ppm) the change in Δmin Ω_{arag} from 0% to 100% CC declines from −0.65 and −0.38, respectively, while Δmin pH declines to −0.129 and −0.093.

The Δmean pH from 0% to 100% CC corresponds to an estimated decline in coral calcification of −7.7% to −18.0% under present day conditions (Fig. 5). Biologically-mediated chemical dissolution is predicted to increase from +13.5% for microbioerosion and +27.9% for clionaid sponges with the changes in mean pH. The Δmin pH from 0% to 100% CC would correspond to a decline in coral calcification of −14.4% to −35.2% and increase in biodissolution of +31.0% to +62.2%. These larger declines

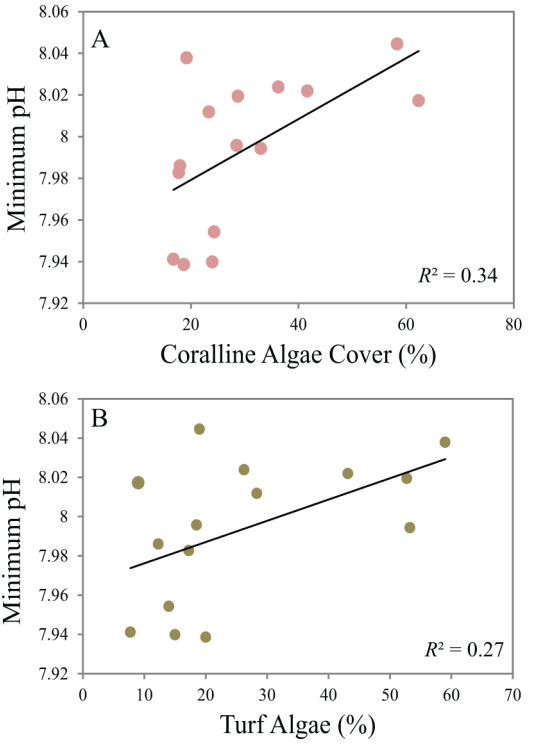

Figure 3. Minimum pH plotted against (A) coralline and (B) turf algae cover for fore reefs.

are associated with the minimum pH values that occur at night, thus these would represent upper bounds to any percent change in rate of calcification and biodissolution. When the model was run for minimum pH normalized to 25 °C, the results were similar though slightly more conservative as $\Delta\text{min pH}_{25}$ from 0% to 100% CC would correspond to a decline in coral calcification of –12.3% to –31.6% and increase in bio-dissolution of +25.3% to +52.9%.

Discussion

The "boosting" of OA impacts by corals, or net lowering of seawater pH, has been shown previously in laboratory and field studies (Anthony et al. 2013, 2015, etc.), but this is the first time that field evidence across multiple sites has been presented. Our results are in line with the pioneering study of Anthony et al. (2013) that showed the magnitude of decline in Ω_{arag} at night due to coral metabolism was 3 to 5 times higher than the increase in Ω_{arag} during the day, leading to an overall net depression of Ω_{arag}. These authors suggested that there would be a 20%–30% increase in OA impacts at night due to added metabolic acidification of corals at high CC sites. Thus, despite the increased variance in pH with higher coral cover, there is an overall net depression over a diurnal cycle due to extreme pH minima at night (Fig. 2B).

We hypothesize that the lower pH values are likely driven by reef metabolism when there is high coral cover, but we acknowledge the fact that many different biotic and

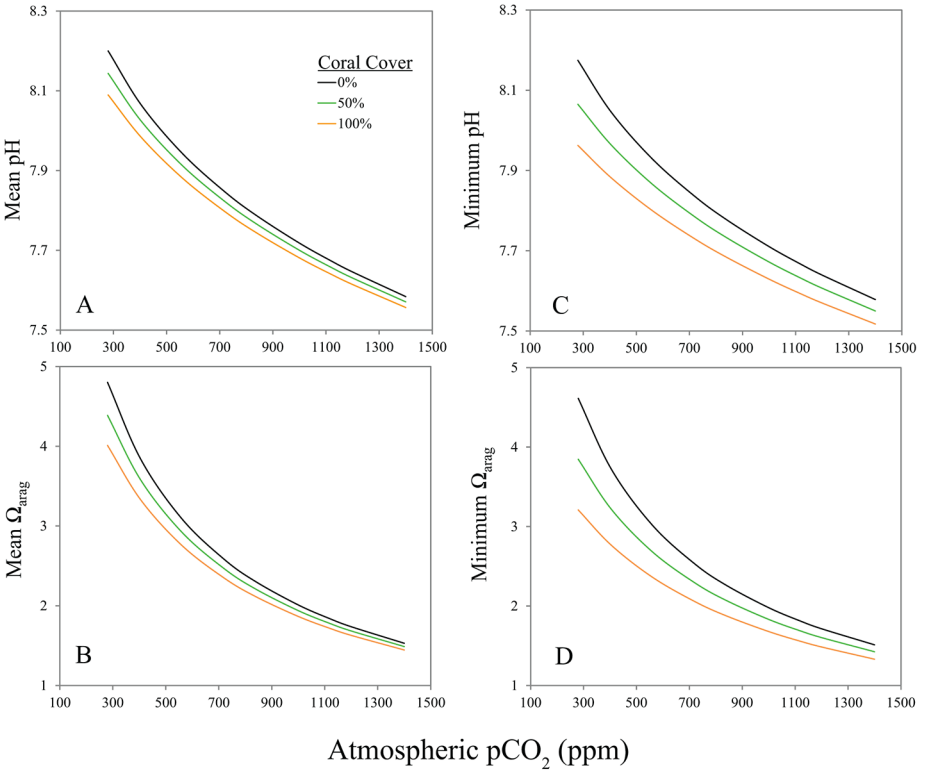

Figure 4. (A) Mean pH, (B) mean Ω_{arag}, (C) minimum pH, and (D) minimum Ω_{arag} as a function of atmospheric CO_2. Black line is 0% coral cover, green line is 50%, and orange line is 100%.

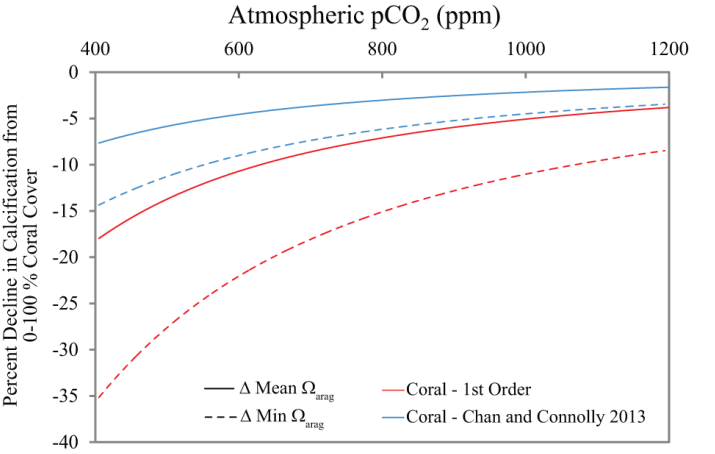

Figure 5. Predicted decline in coral calcification owing to negative feedback from 0% to 100% coral cover. Red line is 1st order relationship between coral calcification and Ω_{arag} whereas blue line is relationship predicted by meta-analysis (Chan and Connolly 2013). Solid line is change due to decline in mean Ω_{arag}, whereas dashed line is change due to decline in minimum Ω_{arag} from 0% to 100% coral cover.

abiotic variables that were not measured in this study influence pH variability on coral reefs. These include, but are not limited to, tides, currents, freshwater inputs (precipitation, runoff, groundwater), residence time, light, upwelling, upstream biological phenomenon like phytoplankton blooms, etc. (*see* Kapsenberg and Cyronak 2019). It seems unlikely that upwelling could be depressing pH, as pH and temperature were not correlated on the fore reefs and were negatively correlated in the lagoons (Online Table S7). A decline in pH associated with upwelling would correspond with a decline in temperature and, thus, pH and temperature would be positively correlated (e.g., Manzello et al. 2008). Nevertheless, there could be larger-scale upwelling processes that are not manifesting in our short-term records but are depressing pH. In this case, the high coral cover and low pH could be related to upwelling acting as a food source (Radice et al. 2019). The other factors highlighted above require more time-intensive, site-based process studies to reconcile.

These pH snapshots taken across a large spatial scale are an important first step toward understanding the real-world impacts of benthic community structure on reef pH variability, which remains poorly understood. However, the short-term nature of the pH time-series data warrants caution, as they require further verification and study. Short-term measurements of seawater carbonate chemistry do not incorporate seasonal and interannual variability, which is key to understanding the threat of OA to any organism or ecosystem (e.g., Manzello 2010). Also, limited sampling poses the risk of data collection during an anomalous event, such as would occur during abnormal weather patterns or phytoplankton blooms. Despite these very real caveats, the patterns we observed were clear and in agreement with both laboratory and modeling work. The focus on remote reefs with minimal anthropogenic impacts suggests that the patterns described herein may differ on reefs that are more disturbed.

The positive trend between coralline and turf algae cover and minimum pH may be due to the much lower metabolic rates vs corals. In other words, as coralline algae become more abundant on a reef (>25% cover, Fig. 3), the resultant modification of the overlying seawater by the reef metabolism declines and pH minima increase. Indeed, reef pavement, composed of turf and coralline algae, has a very small metabolic signal and even exhibits slight dissolution at night which raises pH (Comeau et al. 2016). Similarly, the magnitude of change in Ω_{arag} due to coralline algae was 20%–30% of that caused by similar abundances of corals in the study by Anthony et al. (2013). Laminar growth forms of coralline algae are much less rugose and have lower surface complexity than morphologically complex coral taxa (e.g., branching, foliose, and tabulate growth forms) leading to less biologically-active surface area interacting with the surrounding seawater. The less architecturally complex reef surfaces and lower metabolic rates of reef structures that are dominated by turf and coralline algae are likely key factors in higher minimum pH values with increasing coverage of these two functional groups. There was no relationship between macroalgae cover and pH. Macroalgae cover was generally very low with mean (SE) cover of 6.5% (1.59) and 7.7% (1.46) in the lagoon and fore reefs, respectively, and the maximum observed coverage was 21% (Table 1, Online Table S3). The fact that the GRE targeted remote reef locations far removed from anthropogenic impacts likely played a role in the low coverage by macroalgae, which can be stimulated by nutrient inputs from human activities (Smith et al. 1981). However, this relationship is not always clear cut, as macroalgae coverage can sometimes be higher around uninhabited islands (Smith et al. 2016).

We provide several hypotheses for the lack of any relationship between pH variability and benthic cover in the lagoons. Lagoonal environments tend to have lower flow rates and higher residence times than offshore fore reef environments, which has been hypothesized to drive higher variability (Falter et al. 2013). The signature of the benthic community on the seawater chemistry of lagoons may not be as consistent due to less regularity in water motion, especially for those lagoons with episodic wave or wind driven flow regimes (Hench et al. 2008). Furthermore, the lagoonal water masses have the potential for recirculation and they integrate more than just the coral reef community, potentially incorporating other habitat types like sandy or muddy lagoon bottoms, seagrasses, etc. Similarly, variability in pH may also be reduced when there is longer residence time due to the integration of multiple day/night cycles that can offset the signature of diurnal reef metabolism (Takeshita et al. 2018). In comparison, an offshore fore reef is being impacted by seawater primarily from the open ocean that then traverses the reef in a more unidirectional manner, minimizing recirculation and impacts from other upstream habitats. Lagoonal environments also have lower light levels than offshore fore reefs, with high island lagoons being more turbid than those of atolls (Maritorena and Guillocheau 1996). Rates of photosynthesis and calcification may thus be depressed in lagoons relative to offshore fore reefs at comparable depths owing to lower light, given that lower rates of metabolism have less impact on the CO_2 dynamics of the overlying seawater (Anthony et al. 2013). Thus, we suggest the impact of the benthic community on seawater pH variability is more complicated in restricted environments with variable flow regimes.

Future work is necessary to explore how comparable coral coverage impacts mean reef pH across differing temperatures given that the relationship between these two variables became nonsignificant when pH was normalized to 25 °C. It is likely that normalizing pH to 25 °C artificially represents the interaction of this variable with coral reef communities in situ given that temperature impacts pH thermodynamically, coral metabolism is a function of both temperature and pH, and coral metabolism in turn impacts pH (Jokiel et al. 2014). We argue that the relationship between mean pH and coral cover was not solely thermodynamic in nature despite a lack of correlation at pH_{25} given that there was a relatively even spread of coral cover across temperatures (Online Fig. S3).

The importance of diurnal variability to an organism's response to OA is not well understood, as the limited number of studies have yielded different results for different species (reviewed by Rivest et al. 2017). For corals, diel variability may enhance calcification, potentially ameliorating OA (Dufault et al. 2012, Comeau et al. 2014, Chan and Eggins 2017). This is likely because maximum pH occurs during the day, when coral calcification is highest (Comeau et al. 2014, Chan and Eggins 2017). The minima in pH occur at night and thus would have the most impact on dark calcification (Anthony et al. 2013, Enochs et al. 2018). Dark calcification in corals is not well understood and highly variable, but generally occurs at a rate of about ⅓ that of light-enhanced calcification (Gattuso et al. 1999). As such, the daily maximum pH values have been suggested to be most critical to the overall rate of coral calcification (Chan and Eggins 2017, Enochs et al. 2018). However, there are still few studies that have directly addressed the role of pH variability on coral calcification. In particular, more research is needed to understand how more extreme nighttime pH minima will impact both dark and net calcification of corals.

Other taxa, such as coralline algae, may be negatively impacted by pH variability (Cornwall et al. 2013, Johnson et al. 2019). For those species whose response to low pH conditions does not interact with light, such as fishes, the exposure time and magnitude of stressful conditions will be higher in more variable habitats (Shaw et al. 2013b). Nonphotosynthetic organisms (i.e., azooxanthellate clionaid sponges) that utilize chemical dissolution will likely thus experience the greatest pH driven enhancement at night.

It is still not understood if organisms are responding to minimum, maximum, mean, or some combination of pH, pCO_2, or Ω_{arag} (Shaw et al. 2013b). This is likely different depending on the taxa and physiological processes that are involved. It has been recently argued that net photosynthesis and coral calcification lead to changes in Ω_{arag} and not the other way around (Jokiel et al. 2014, Cyronak et al. 2016). These authors suggest that hydrogen ions, a byproduct of calcification, must be removed as they build up in coral tissues. This process becomes more energetically costly as OA progresses, which leads to the decline in calcification with decreasing pH. The correlation between calcification and Ω_{arag} is argued to exist because $[H^+]$ and Ω_{arag} are correlated (Jokiel et al. 2014).

Despite the OA research "boom" of the past decade, much remains to be resolved with respect to the impacts to coral reefs. Future research is necessary to understand the importance of these lower minimum pH values with higher CC to the large diversity of coral reef organisms and physiological processes impacted by pH. The large-scale field data here show that the magnitude and duration of exposure to depressed pH from OA may be greatest on reefs with the highest CC. Future work is necessary to understand if corals and other taxa are able to locally adapt or acclimatize to highly variable pH, which could make them less susceptible to OA. Corals that experience naturally higher and more variable temperatures do show such capacity and appear better suited to cope with ocean warming (Palumbi et al. 2014, Manzello et al. 2019). The overarching goal of the GRE was to examine factors that promote coral reef resilience to aid in local management and conservation. Thus, the finding that the coral reefs with the highest coral cover were experiencing the lowest pH values may at first appear paradoxical. These high coral cover reefs also had the greatest pH variability and pH range. Despite the overall net lowering of pH and most extreme low pH values, the large range and variability may be more indicative of a healthy, thriving coral reef than overall mean pH or pH minima.

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